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THE ECOLOGICAL RELATIONSHIPS OF THE DRAGONFLIES OF THE BASS ISLANDS OF LAKE ERIE[1]

Clarence H. Kennedy
Ohio State University

The dragonfly fauna of the Put-in-Bay region is one of the most meager the writer has seen, but its very lacks and limitations make it one of the most interesting. The ecological groupings are so sharply defined that their relationships are outstanding. This obvious grouping of the species in the field leads us directly to a parallel division of the discussion as follows: (1) The lake species and their origin. (2) The pond species, their origin, and their succession as the ponds age. (3) The constant pressure of the pond species into the habitat of the lake species.

The data cover the time from June 20 to August 1, 1921, the opening and closing dates of the Lake Laboratory.

1. The Lake Species and Their Origin

The biological station of Ohio State University is located at Put-in-Bay on South Bass Island, which is approximately five miles from the southern shore of Lake Erie. South Bass is the southernmost of the group of Bass Islands, which, with Kelly's, Pelee, and numerous smaller islands, stretch as an archipelago north to the Canadian shore (see the map, fig. 1). All are low limestone tables whose highest contours seldom rise more than ten feet above the lake surface. The island shores, except for a few bays with sand or gravel beaches, are perpendicular limestone cliffs about whose bases the waves beat continuously among the ledges and boulders (see fig. 2). The water in this western end of Lake Erie is only thirty feet deep; in fact, Lake Erie is the shallowest of the Great Lakes. Soundings show that the greater extent of this shallow bottom is covered with clay and sand. The strictly lake environment then, while great in extent, is extremely monotonous for a diversified Odonate fauna. It is, in fact, a very simple but very special environment consisting of the rocky shore line and flat lake bottom. As even thirty feet of water is too deep for Odonate larvae, this great area of bottom is excluded as dragonfly environment, leaving the rocky, wave-torn cliffs and boulder shores with their occasional sand or pebble beaches as the only freehold for these insects. Because of the many miles of such rocky shores the lake Odonata are still very numerous, but are reduced to the very few species that can survive among wave-washed rocks or perhaps that can emerge into adult life successfully on such shores.

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Along these rocky shores only four species of dragonflies are abundant. These are the little gray *Argia moesta,* the large *Gomphus plagiatus* and *Neurocordulia yamaskinensis,* and the great black and yellow *Macroma illinoiensis. Argia moesta* occurs in great numbers on all islands high enough to have a cliffy shore. It occurs in numbers also on East Sister, where the entire shore line is of coarse gravel. The other three occur in less numbers, yet are abundant. *Neurocordulia yamaskinensis* is crepuscular in

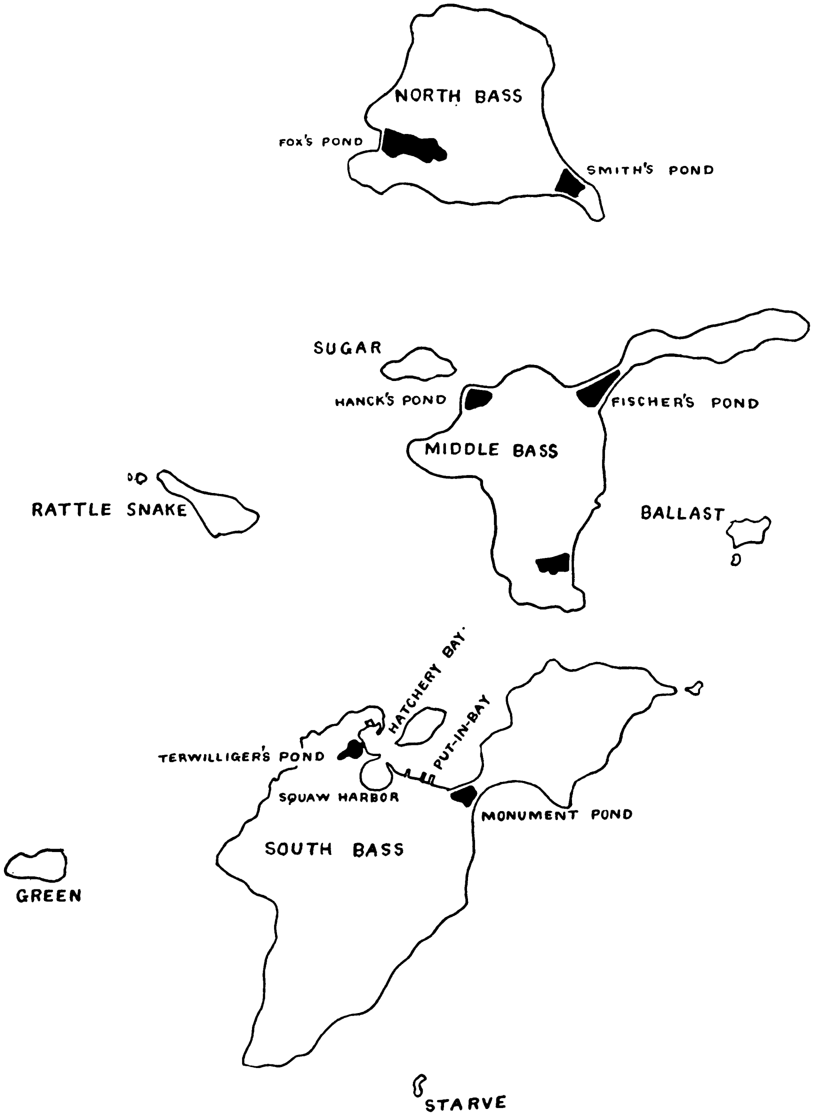

FIG. 1. Map of the Bass Islands of Lake Erie, showing the ponds and harbors.

habit, flying only at sunrise or sunset, or occasionally on cloudy days. It feeds on the great swarms of aquatic insects that come out of the lake each evening, while it spends its daylight hours sleeping in the trees. The other species are diurnal and roam the fields and woods for a more general diet.

Along the sand and pebble beaches occur *Gomphus vastus* and *Gomphus fraternus,* which are typical lake species (see fig. 3). Though very much restricted in its breeding sites because of the very few beaches, *Gomphus vastus* in season is the most abundant of the large dragonflys. *Gomphus fraternus* is seldom seen or caught.

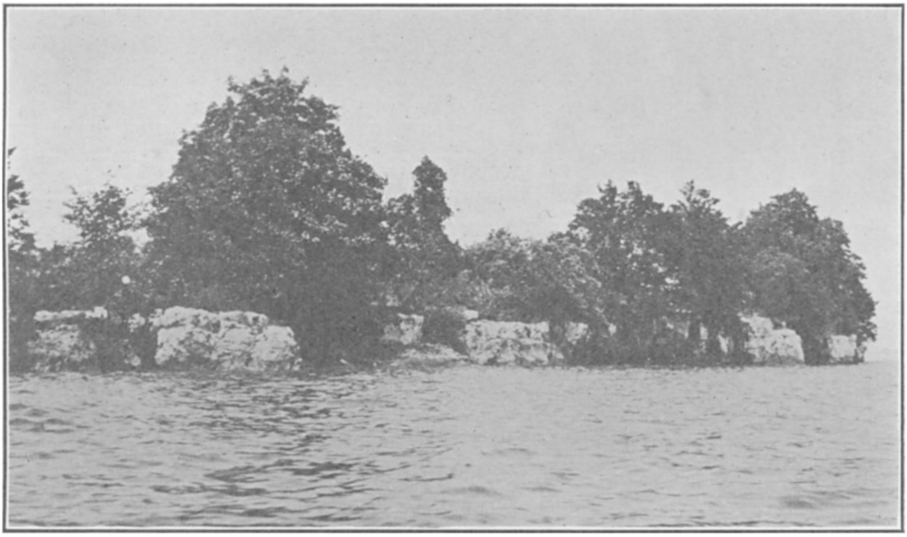

FIG. 2. The vertical limestone shore of Rattle-Snake Island. Habitat of *Gomphus plagiatus, Neurocordulia, Macromia* and *Argia*

The nymphs of the three lake species of *Gomphus* burrow in the mud and sand of the lake bottom. Why *plagiatus* should prefer such bottom near a rock shore, and the other two a bottom bordered by a beach, is not known. The nymphs of the other lake species are long-legged and scramble for a living among the rocks.

The origin of the lake species is similar to that of the other lake-shore inhabiting aquatic insects. These lake species have probably originated from the streams of the surrounding mainland. *Neurocordulia* probably comes from the streams of southern Canada, and *Argia,* the three *Gomphus,* and *Macromia* come from the streams of the Northern States. All the strictly lake species adapted to the well aerated and tempestuous waters of the shore are then true stream species. The three *Gomphus* larvae avoid the rough waters by their burrowing habits; the other three species have very vigorous long-legged larvae with strength enough to take care of themselves in spite of the waves.

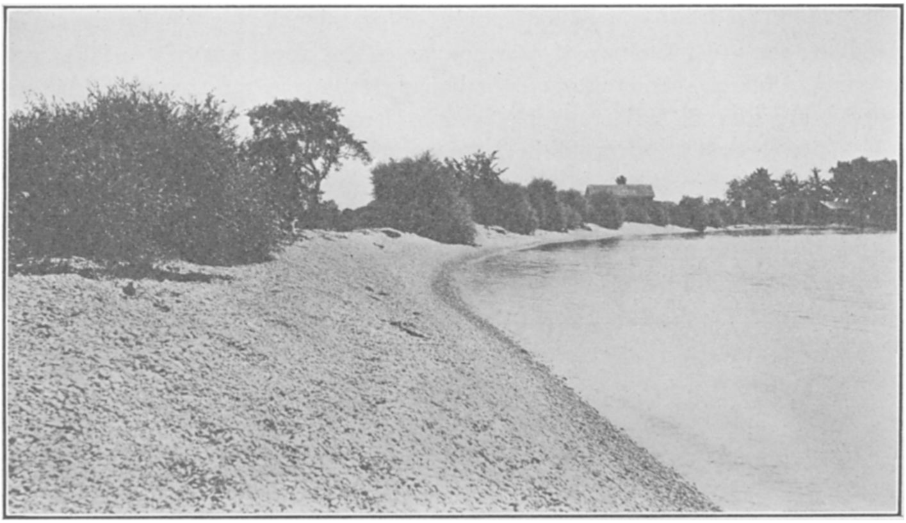

FIG. 3. Gravel bar closing Hanck's Pond on Middle Bass Island. Habitat of *Gomphus fraternus* and *Gomphus vastus*

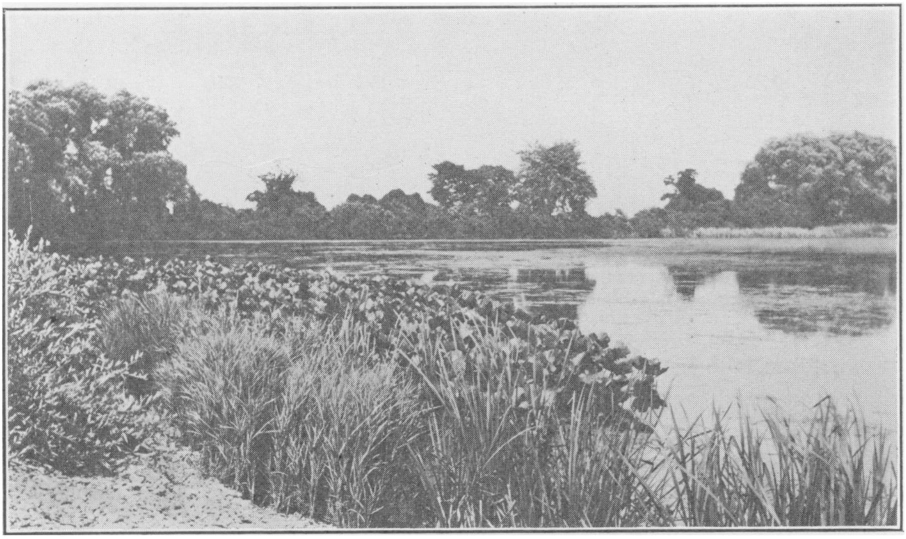

FIG. 4. Hanck's Pond, Middle Bass Island. This pond is at the peak of its development, supporting the full list of pond dragonflies

2. THE POND SPECIES, THEIR ORIGIN, AND THEIR SUCCESSION AS THE PONDS AGE

A further description of the islands is desirable to correctly place this series of species. The islands in their primitive condition were covered with hardwood forests that had cedar groves about their edges where the soil was shallow. Seven ponds occur on the three main islands: two on South Bass, three on Middle Bass, and two on North Bass. (Pelee and Kelley's Islands were not explored in this study.) These ponds are peculiar in their origin and development. All seem to have originated as small bays, which later have been cut off from their lake connection by gravel bars shoved up by wave and ice action.[1] They seem to have originated contemporaneously after the retreat of the ice, but some have aged more rapidly than others, so that a graduated series can be easily traced from the clean and open Put-in-Bay to the ecological climax of a grassy meadow or a hardwood forest protected from the lake by a gravel dyke, as exemplified in Fox's pond at Manilla Bay on North Bass (see figs. 5 and 6).

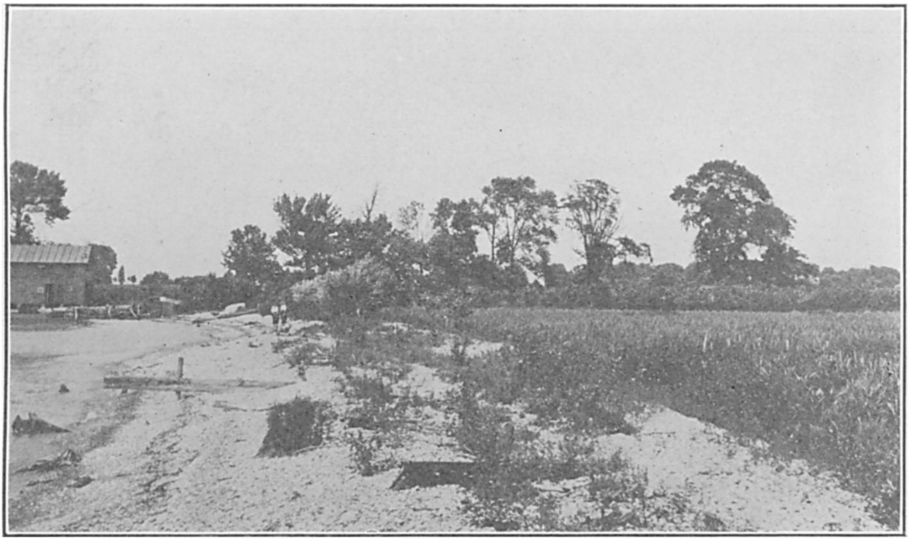

FIG. 5. Fox's Pond, North Bass Island. This is a pond in its old age, after it has become a Sparganium and sedge marsh, with the *Sympetrum* and *Lestes* dominant.

More specifically their development can be shown in the following series:

1. Put-in-Bay, South Bass. Open to the lake, deep, bottom of mud and sand, shores rocky or gravelly. Vegetation limited to diatoms and other algae.

2. Hatchery Bay, South Bass. As in No. 1, but so protected by submerged bars that *Elodea, Valisneria,* and *Potamogeton* flourish.

3. Squaw Harbor, South Bass. As in No. 2, but so protected by partially emergent bars that water-lilies and sedges grow about its somewhat mucky edges.

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[1] The origin of these and the mechanical forces involved are being worked out by Prof. F. H. Krecker.

4. Terwilliger's Pond, South Bass. Enclosed by a high bar except for a small channel. Vegetation as in No. 3, but the mucky shores well developed into a *Sparganium* and *Scirpus* marsh.

5. Hanck's Pond, Middle Bass. As in No. 4, but the bar completely closed and the shores of the pond so developed that the higher borders are grassy (see figs. 3 and 4).

6. Fox's Pond, North Bass. A marsh protected from the lake by a high gravel beach and entirely filled with muck except for a few square yards of shallow water containing *Polygonum, Myriophyllum,* etc. The central area of the marsh is covered with *Sparganium,* which gives place as one goes landward, first to sedges, then grasses, and finally to a growth of ash (see figs. 5 and 6).

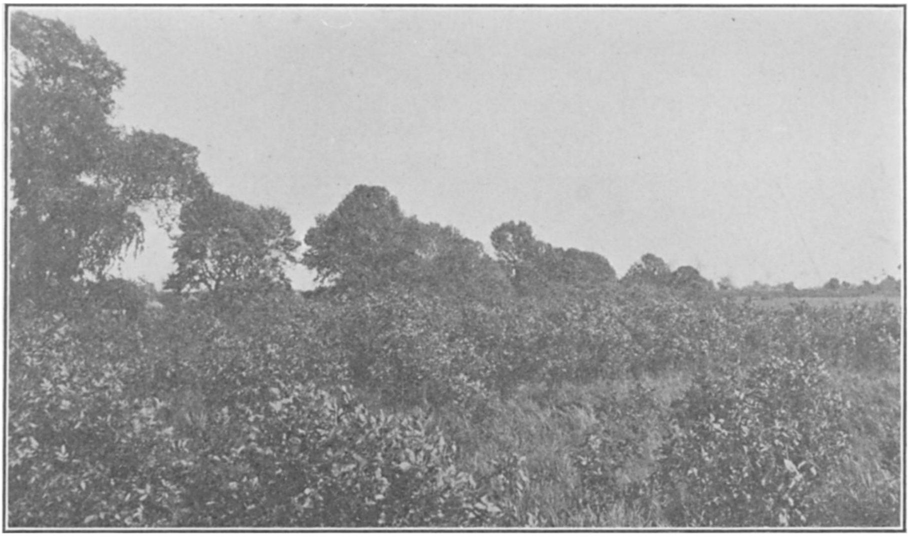

FIG. 6. Fox's pond; showing the last stage in the life of a pond. The grassy edges are being invaded by grass. No dragonflies

The following species of dragonflies are found so regularly about these ponds that they may be considered as fixed items in the pond fauna:

1. *Lestes forcipatus*
2. *Lestes rectangularis*
3. *Ischnura verticalis*
4. *Enallagma carunculatum*
5. *Enallagma ebrium*
6. *Enallagma exsulans*
7. *Enallagma signatum*
8. *Anax junius*
9. *Sympetrum obtrusum*
10. *Sympetrum vicinum*
11. *Leucorrhinia intacta*
12. *Erythemis simplicicollis*
13. *Pachydiplax longipennis*
14. *Libellula luctuosa*
15. *Libellula pulchella*
16. *Plathemis lydia*
17. *Tramea lacerata*

The following pond species appears to be strays that are not abundant, or are perhaps not seasonal from June 20 to August 1:

1. *Lestes disjunctus*
2. *Lestes unguiculatus*
3. *Lestes uncatus*
4. *Nehalennia irene*
5. *Epiaeschna heros*
6. *Aeschna constricta*
7. *Epicordulia princeps*
8. *Sympetrum rubicundulum*
9. *Libellula semifasciata*

This pond fauna shows a definite succession from the open lake fauna of such open harbors as Put-in-Bay, where no pond species occur, to the *Sympetrum-Lestes* climax in the aged ponds such as Fox's on North Bass. Perhaps this can be most easily shown by giving the Odonate fauna of the six stages of ponds just listed.

1. *Put-in-Bay.* This contains the pure lake fauna, consisting of *Argia moesta, Gomphus vastus, Neurocordulia yamaskinensis,* and *Macromia illinoiensis.*

2. *Hatchery Bay.* A mixed fauna consisting of the lake fauna as in Put-in-Bay, to which have been added the following that live in the patches of aquatic weeds: *Enallagma carunculatum* very common, *Enallagma exsulans* and *Ischnura verticalis* less common, with *Enallagma ebrium* and *Epicordulia princeps* as strays on Gibralter Island in the Bay.

3. *Squaw Harbor.* Individuals of the lake species few, but the pond species increased by the addition of *Ischnura verticalis* in numbers, with a few *Anax junius.*

4. *Terwilliger's Pond.* No lake species whatever. The following purely pond species abundant:

Ischnura verticalis
Enallagma ebrium
Enallagma exsulans
Enallagma carunculatum
Enallagma signatum
Anax junius
Libellula luctuosa
Libellula pulchella
Tramea lacerata

The following occasionally taken: *Lestes rectangularis, Enallagma hageni,* and *Epicordulia princeps.*

5. *Hanck's Pond.* This pond is at its richest stage as far as flora and fauna are concerned (see fig. 4). It contains all the species found in No. 4, and, because of its greater area of surrounding marsh, adds in abundance such species as:

Lestes rectangularis
Lestes forcipatus
Sympetrum obtrusum
Sympetrum vicinum
Pachydiplax longipennis
Erythemis simplicicollis
Leucorrhinia intacta
Plathemis lydia

Fischer's Pond of Middle Bass and Smith's Pond of North Bass come in this same category.

6. *Fox's Pond.* This is no longer a pond, but a marsh with a few inches of water in some small, open places in its center. The land edges of the marsh have already become so built up that they are occupied by sedges, grasses, and trees (see figs. 5 and 6). The main area of the marsh is Sparganium, in which flourish *Sympetrum obtrusum, Sympetrum vicinum, Ischnura verticalis,* and *Lestes forcipatus* in large numbers. Occasional individuals of *Enallagma hageni, Lestes rectangularis, Lestes uncatus, Lestes unguiculatus, Anax junius,* and *Sympetrum rubicundulum* occurred among these abundant species. In the open, shallow pools of the center of the marsh a few individuals of *Aeschna (constricta ?), Libellula pulchella,* and *Pachydiplax longipennis* managed to persist.

The diagram, figure 7, shows the succession of species as the open harbor ages into a pond and finally dries into a marsh. Not enough is known of the habits and life histories of these to more than suggest what the controlling factors may be. The first five species, which cling to the lake shores, demand moving water; perhaps their respiratory apparatus needs the aid of well-aerated water. These shore dwellers have either very short legs and get protection from the waves by burrowing in the lake bottom or have unusually long legs so that they can handle themselves among the wave-washed rocks. The species of *Gomphus* are the burrowers, while *Argia, Neurocordulia,* and *Macromia* are the long-legged scramblers. In the pond species *Anax* and *Aeschna* prefer vegetation with vertical stems, where the female can back down into the water to oviposit and the larvae can roost in a vertical position while lying in wait for prey. The marsh species, *Lestes* and *Sympetrum,* represented by the last six of the diagram, are adjusted to intermittent marsh conditions by the fact that they all probably pass the winter in the egg stage. *Lestes* eggs laid in the late summer and fall can dry out and then hatch with the first spring rains, probably also those of *Sympetrum.*

3. THE CONSTANT PRESSURE OF THE POND SPECIES INTO THE HABITAT OF THE LAKE SPECIES

Pond species remain such partly because the females prefer to oviposit in quiet water or where there is vegetation in the water. None of them oviposit with any regularity along the very extensive rocky shores of the islands. Yet there are islands in this group which possess only rocky shore lines and no vestige of ponds, but which annually yield a few individuals of strictly pond species to the collector's net. This was first noticed in the south end of South Bass, two miles from the nearest pond (Terwilliger's), where the island shores are high cliffs rising directly from the lake surface. Here *Ischnura verticalis* was common, and several *Anax junius, Epiaeschna heros,* and *Pachydiplax* were taken. *Epicordulia princeps, Libellula pulchella,* and

Libellula semifasciata were seen. Ten miles to the south lay the great Sandusky Bay marshes. Undoubtedly a few of these had been blown across, but apparently the majority were the offspring of such wanderers rather than the original emigrants. The *Anax* were tenerals as well as some of the Ischnuras. These must have emerged from the near and forbidding lake shore with its waves and rocks. The most acceptable explanation is that fertile females wander from the ponds on the north side of the island or across the lake from the Sandusky marshes and manage to oviposit along the rocky shore. This could be done on calm days. Some of the young would probably survive, just enough to keep this end of the island provided with a few strictly pond species. The following small islands provide similar but more striking evidence:

East Sister Island. The nearest pond to this island is about seven miles south on North Bass. The shore is a coarse gravel beach, though the island is many acres in extent. Yet *Nehalennia,* the Enallagmas *ebrium* and *caruncülatum, Pachydiplax* and the Sympetrums, *obtrusum, rubicundulum,* and *vicinum,* were represented on the island by a few individuals each.

Hen Island. This island is about twenty acres in extent with high rocky shores. The nearest pond is on North Bass, about five miles distant. On Hen Island were found a few individuals each of *Nehalennia, Lestes rectangularis, Aeschna constricta, Libellula pulchella,* and *Plathemis lydia.*

Big Chick Island. This is a gravel and cobble reef with the gravel piled up about ten feet high. It is perhaps an acre in extent and contains one live tree, a dozen stalks of *Scirpus,* and a few cucumber vines. It is a tern roost harboring thousands of these birds. The nearest island is a mile distant, the nearest pond about five miles. Yet an *Ischnura* and two Enallagmas were collected on the lee side of the tree in 1920. However, in 1921 none were found.

Ballast Island. This is a small island, perhaps ten acres in extent, but with rocky shores, and it lies one mile east of Middle Bass. Besides the usual lake species found on all the islands, *Ischnura,* the Enallagmas, *ebrium* and *exsulans,* and *Sympetrum obtrusum* were found.

Rattle Snake Island. This island is about a mile long, but is surrounded on all sides by precipitous limestone cliffs. The nearest pond is at least two miles east of it. On it were caught in 1920 a female *Enallagma* and a *Pachydiplax.*

Sugar Island. This is about a quarter of a mile long, is low, but has clean, rocky shores, the eastern end being sandy and a great place for *Gomphus.* In one spot low enough to be continuously renewed by seepage from the lake was a small puddle not over ten feet long and three wide. In its neighborhood were taken *Ischnura,* the Enallagmas, *ebrium* and *carunculatum, Anax, Pachydiplax* and the Libellulas, *luctuosa,* and *pulchella.* This

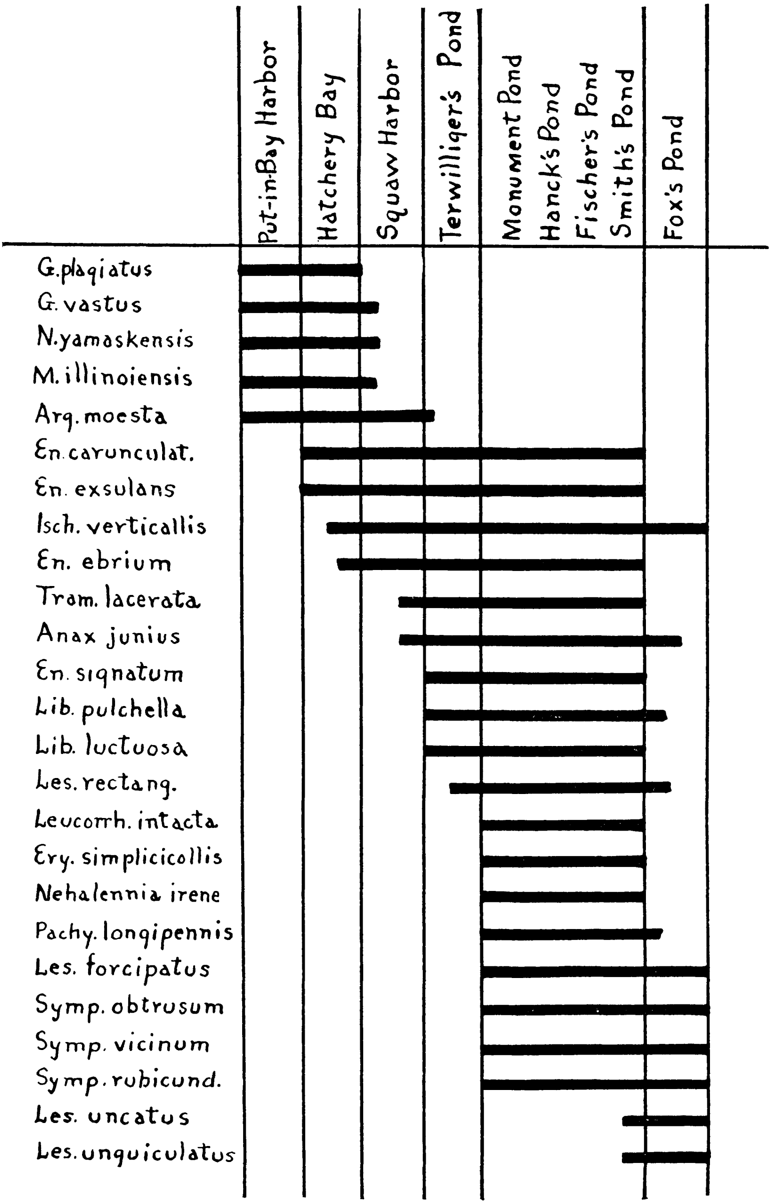

FIG. 7. The succession of dragonfly species as the ponds develop and then age

shows how even the smallest of suitable waters are sought out. The nearest pond was nearly a mile distant on Middle Bass.

It is interesting to note that the lake species are all put by systematists low down in Odonate phylogeny, while the majority of the larger pond species are in the *Libellulinae,* which is the latest and highest of the subfamilies of dragonflies. This means that the lake species are specialized remnants of a preceding fauna, of which the pond species have been already largely displaced by the very modern *Libellulinae.* Ponds are the most acceptable Odonate habitat because of their quiet waters and abundance of dragonfly food, so the later and better forms of Odonata supplant the more primitive species about ponds first.

In more detail: the three Gomphines are exceedingly specialized in the burrowing habit of the larvae, which protects them from the currents and the waves, in the protective coloration of the adults, and in the spatulate abdomen of the latter, which enables them to dodge easily along narrow streams. These are members of the family *Aeschnidae,* which reached its climax before or in early Tertiary times. *Neurocordulia* and *Macromia* are specialized in their long-legged, spider-like larvae that can maintain themselves among the wave-washed rocks, also in the crepuscular habits and cryptic coloration of the former, and in the great wing speed of the latter, which is one of the swiftest dragonflies. These are both in the subfamily *Cordulinae,* a primitive and almost extinct branch of the *Libellulidae,* from which the present dominant *Libellulinae* have probably developed. *Argia* is a remnant of a small group of damselflies that probably reached their climax in the Eocene. For a damselfly its larvae have long legs, while its adults oviposit in wet drift. These all have a long life history of from one to three years.

The pond *Libellulinae* have a life history never longer than one year, and in some species only three months. They are very active hunters and in this short, fast life outlive the specialized, older, and slower *Aeschnidae* and *Cordulinae* of the lake shores. It is interesting that two *Aeschnidae, Anax,* and *Aeschna constricta,* still hang on in the ponds in competition with the *Libellulinae. Anax* has speeded up its life cycle to three months, while *Aeschna constricta,* which is the most widely spread species of a genus which has a dozen species that still persist about the ponds and streams on the northern edge of the main range of the *Libellulinae,* has a nymph that is the last word in savage voraciousness. The *Libellulinae* have probably originated about the ponds of the tropics, where the subfamily is wonderfully rich in pond forms, but there they have already begun to develop specialized stream species. Apparently they are spreading as pond species into the temperate zones, but have not occupied these long enough to have developed a series of specialized stream species there. Curiously enough, some of the more specialized stream *Libellulinae* of the tropics resemble the stream-inhabiting Gomphines of the north in the burrowing habits of their larvae and the spatulate abdomen of the adult. The *Libellulinae* simply outlive the *Aeschnidae* and the *Cordulinae.* Their larvae are generalized so that they are well off on a mud bottom, in trash, or amongst vegetation.

The pond damselflies are all high in the phylogeny of that group as compared to the low position of the lake shore *Argia moesta*. So their case is parallel to that of the dragonflies.

The marsh species, the Sympetrums and the Lestes, are again specialized. They each have one brood a year, and the Lestes, and probably also the Sympetrums, pass the winter in the egg stage. Lestes oviposits in the late summer or fall and the eggs hatch with the first spring rains. This adjusts them to marshes that have a habit of drying out in the fall of the year. While many other species may hang about a marsh during a series of wet years, a single dry fall must wipe out such unadapted species.

Our data cited above indicate that already these modern *Libellulinae* are crowding into the habitat of the lake species, while there is no data to indicate that the lake species are crowding similarly into the ponds. Our data show also that these particular pond species probably will never successfully colonize the lake shores. As in the tropics, the lake shores will eventually be colonized by specialized *Libellulinae*.